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NOCTURNALITY AS A DEFENSIVE BEHAVIOR IN THE RAT: AN ANALYSIS IN TERMS OF SELECTIVE ASSOCIATION BETWEEN LIGHT AND AVERSIVE STIMULATION

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One striking aspect of the rat's daily activity pattern is its strong nocturnal tendency. The present research tests the assumption that nocturnality in the rat serves a defensive function. If nocturnality represents a form of defense, the rat may associate light with aversive events more readily than it associates dark with aversive events. Experiment 1 examined this hypothesis in terms of the rat's foraging behavior while living in an operant chamber. Electric footshock delivered to the grid floor near the response lever simulated the influence of predation during feeding. The results indicated that foraging behavior in the rat is sensitive to the risk of predation. Rats that had shock paired with either the light or dark phase reorganized their meal taking and reduced time spent at risk. However, the finding that the largest changes in foraging occurred when shock was delivered exclusively during the dark phase did not support the hypothesis that nocturnal feeding is a defensive behavior and was not indicative of a selective association between light and aversive events. Similar conclusions were reached when the defensive behavior freezing was used as the discriminative response in differential conditioning studies. Rate of differentiation was faster when shock was paired with a dark phase CS, relative to pairings with a light phase CS (Experiment 4). Rats failed to show differential freezing in a light S+ chamber and a dark S- chamber (Experiment 2), but did so with S+ and S- conditions reversed. Similar results with a light or dark chamber paired with a food US (Experiment 3) suggested two things: first, rats that acquired the discrimination when light phase signaled shock may have relied on endogenous cues rather than light/dark per se; second, the results obtained with pairings of darkness and shock were not indicative of a selective association between darkness and aversive events.

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Traditionally, psychologists interested in the study of animal learning and behavior have conducted research under the assumption that the choice of particular combinations of stimuli (CSs and USs) and responses would not be critical in determining the outcome of their experiments. This kind of thinking stems from the belief that there are general laws of learning that apply in all varieties of experimental situations. Some psychologists, however, (e.g., Garcia & Koelling, 1966; Shettleworth, 1983) have brought attention to a growing body of literature that strongly suggests that all combinations of stimuli and responses do not have an equal potential for association. Rather, in many cases associations appear to be selective (LoLordo, 1979) in the sense that some combinations of stimuli or combinations of stimulus and response are much more readily related than are other combinations.

For example, Garcia and Koelling (1966) demonstrated that certain CSs are more easily associated with some USs than with others. In their classic aversive conditioning study, rats received pairings of a compound CS (taste cues plus audio/visual cues, both present during drinking) with either a shock US or a US that induced illness. When the individual CSs were tested it was found that rats receiving the shock US suppressed their drinking much more when tested with the audio/visual CS than when tested with the taste CS. Conversely, rats made sick by irradiation or lithium chloride treatment suppressed their drinking significantly more when tested with the taste CS than when tested with the audio/visual CS. Garcia and Koelling's work has been taken as evidence for the phenomenon of CS-US relevance, or belongingness (Seligman, 1970). All combinations of stimuli are not equally likely to be associated: Some CSs seem to be more related to some USs.

The avoidance learning literature of the 1950s and 1960s provides a good example of a case of selective association between stimulus and response. Reports of successes and failures to train avoidance behavior seem to depend on the response required. For example, Maatsch (1959) reported rapid acquisition of a one-way running response to avoid aversive stimulation. This contrasts sharply with Meyer, Cho, and Wesemann's (1960) observation of slow and erratic learning when bar pressing was required to avoid electric shock. In 1970, Bolles' species-specific defense reaction (SSDR) theory offered an explanation that could account for these discrepancies. Bolles predicated his theory on the assumption that fear severely restricts the rat's behavioral repertoire to a small set of innate behaviors that the rat uses to defend itself in the wild. For the rat, these species-specific defense reactions include freezing, fleeing, and defensive fighting. This explained why the rat appeared to learn the avoidance response contingency quite readily if the required response was an SSDR (e.g., running), but the rat had great difficulty if a response other than an SSDR was required (e.g., bar pressing).

Bolles' (1970) account of the avoidance learning literature not only indicates that certain stimulus-response associations are more readily

formed than others, but it also suggests that aversive motivation will be most appropriately examined in terms of an analysis of defensive behaviors (Bolles & Fanselow, 1980; Masterson & Crawford, 1982). Thus, within the context of the rat's defense system, the present research continues to examine the selective nature of the associations formed when a rat is confronted with an aversive situation. This research takes, as its starting point, the functional assumption that nocturnality in the rat is a component of its defense system and subjects this assumption to empirical testing. Although others have suggested that nocturnal feeding has the adaptive function of avoiding diurnal predators (Curio, 1976; Daan, 1981; Vilchez & Echave Llanos, 1971), they have not subjected this assumption to empirical testing. One implication of saying that the rat's tendency toward nocturnality represents a form of defense is that associations between light and dark and aversive events should be selective. The possibility that associations are more easily formed between aversive events and light than between aversive events and dark will be examined in situations where different forms of defensive behavior are exhibited. Allison, Larson, and Jensen (1967) have provided some support for this hypothesis. They reported that although the rat's preference for black was increased if the animal was shocked in the white compartment of a black/white box, the preference was weakened but not reversed if the animal was shocked in the black compartment.

We (Fanselow & Lester, 1988) have suggested an analysis of the defense system based on the prey's perception of its location on a "predatory imminence continuum" (p. 4). Predatory imminence reflects the prey's physical (Ratner, 1967) and psychological distance from the predator. At one end of the continuum, predatory imminence is at its lowest possible level (e.g., when a rat is in its burrow) and the prey's behavior is thought to reflect a preferred activity pattern of nonaversively motivated behavior (e.g., mating, nursing, and nest maintenance). At the other end of the continuum, predatory imminence is at its highest level as the predator makes the kill. In between these two points, increasing levels of predatory imminence force the prey animal to abandon its preferred activities long enough to engage in defensive behaviors that reduce the probability of further increases in predatory imminence. It is hypothesized that different defensive behavior patterns would be necessary at different points along the continuum and that the environmental stimuli controlling these behaviors would also vary along the continuum (see also Rovee, Kaufman, & Collier, 1977).

We have described three points along the predatory imminence continuum. First, *preencounter* defensive behaviors are those that the prey animal engages in when the risk of predation is present although no specific predator has been detected. The class of behaviors Kruuk (1972) and Edmunds (1974) have described as primary defensive behaviors is most similar to this category. Preencounter defensive behaviors have functions other than defense, but they are organized in a

manner that reflects the potential for predation. For example, when a rat forages for food, predatory imminence is higher than it is when the rat is in its burrow. The rat may organize its foraging behavior to reduce the probability of encountering a predator. We have begun to examine preencounter defense by studying changes in total consumption, meal frequency, and meal size as a function of the risk of predation (Fanselow, 1989; Fanselow & Lester, 1988; Fanselow, Lester, & Helmstetter, 1988). Second, *postencounter* defensive behaviors refer to the prey animal's responses to a predator that has been detected. These forms of defense are similar to the class of behaviors Edmunds (1974) has termed secondary defensive behaviors. At this point along the continuum, predatory imminence is relatively high and the sole function of these behaviors is to avoid contact with the predator. These are the behaviors Bolles (1970) described as species-specific defense reactions. For the rat, the dominant postencounter defense seems to be freezing (Fanselow, 1986; Fanselow & Lester, 1988). In the laboratory, this postencounter defensive behavior is observed when rats are confronted with a cat (e.g., Blanchard & Blanchard, 1971; Lester & Fanselow, 1985) or when exposed to stimuli that have previously been paired with shock (e.g., Bouton & Bolles, 1980). At a third point along the predatory imminence continuum, *circa-strike* defensive behaviors occur just prior to, during, and just after the predator makes physical contact with the prey animal. These behaviors occur when predatory imminence is very high and presumably represent a final effort to avoid or escape from the predator. For example, Hirsch and Bolles (1980) reported that deermice *(Peromyscus maniculatus gambeli)* froze when placed in close proximity to a gopher snake, but they engaged in a "last second vertical leap *as the snake was striking"* (p. 81, emphasis added). An analogous situation may occur in the laboratory when a freezing rat is presented with an electric shock or a sudden light/noise/vibration compound stimulus. Fanselow (1982; 1984) has described the unconditional response to such stimuli as an "activity burst."

Within this organizational framework then, the present research attempts to examine if light provides better stimulus control than dark over two very different defensive responses as representative examples of different stages of defense. The goal of these studies is to explore the possibility that nocturnality is an integrated component of the rat's defensive behavior system (Fanselow & Lester, 1988). The first experiment focuses on the rat's preencounter defensive strategy for foraging when at risk of predation. The second and fourth experiments examine freezing as an example of postencounter defensive behavior. The third experiment tests the same cues (light versus dark) when food rather than shock is the unconditional stimulus (US).

Experiment 1

Our laboratory studies of foraging (Fanselow & Lester, 1988;

Fanselow et al., 1988) have employed a design developed by Collier and his colleagues (e.g., Collier, 1981; Collier, Hirsch, & Kanarek, 1977). This design features a rat living in, what is termed, a "closed economy" (Collier, 1981, p. 77). It is a closed economy in as much as the rat has control over its own foraging behavior. The rat lives in the apparatus 24 h a day and bar presses to obtain all of its food. The rat thus determines how many meals it will take and how large each meal will be.

Collier, Hirsch, and Hamlin (1972) have studied the way that rats pattern their meals when living in a closed economy. They noted that rats decreased meal frequency with a compensatory increase in meal size when the work required to procure each meal was increased. Based on these findings, we hypothesized that an increase in a different kind of cost might have similar effects on meal patterning. Whereas Collier et al. manipulated cost by varying the number of bar presses required to gain access to food, we manipulated cost by varying the risk of predation during foraging. Frequency of electric footshock was used to model predatory risk. The appropriateness of electric footshock as a model of predation is evidenced by the findings that stimuli associated with shock (e.g., Fanselow, 1980; Fanselow & Baackes, 1982; Lester & Fanselow, 1985) and the presence of a cat (Blanchard & Blanchard, 1971; Bronstein & Hirsch, 1976; Lester & Fanselow, 1985; Satinder, 1976) both elicit the SSDR freezing and an opioid form of analgesia. Furthermore, there seems to be some overlap in the physiological mechanisms controlling freezing to these two types of stimuli because lesions of the amygdala result in a decrease in freezing to stimuli associated with shock and to a cat (Blanchard & Blanchard, 1972).

Results from our studies showed that rats responded to increases in the risk of electric shock in the foraging environment by decreasing meal frequency and increasing meal size (Fanselow & Lester, 1988; Fanselow et al., 1988). Overall intake was only minimally reduced but the rats tended to gain or maintain weight over the course of the experiment. These results indicated that the rat's foraging behavior is sensitive to the presence of aversive stimuli. When shock was delivered in the foraging environment, rats decreased the risk of aversive stimulation by spending less time procuring meals at the response lever (thereby spending less time on the shock grids), but they did not sacrifice caloric intake in the process. These findings are in agreement with the predictions derived from the predatory imminence model and are similar to the results that Collier et al. (1972) obtained with increases in procurement costs.

However, because shock was delivered at random times over the 24-h period, these studies did not allow us to examine the most salient feature of the rat's foraging behavior. The freely feeding rat takes about 70% of its meals during the dark phase of a 12:12 light/dark cycle (Barnett, 1975; Collier et al., 1972; Levitsky, 1970; Richter, 1967; Rosenwasser, Boulos, & Terman, 1981; Siegel, 1961; Zucker, 1971). This feeding pattern is under the influence of an endogenous circadian pacemaker that is typically entrained to changes in the environment's

light/dark cycle but, by definition, does have its own free-running period of about 24 h (Richter, 1965). Zucker (1971) reported that rats gradually reverse their feeding rhythm in response to an abrupt inversion of the light/dark cycle. Rosenwasser et al. (1981) found that even the dusk and dawn peaks characteristic of nocturnal feeding show persisting circadian rhythms under conditions of constant dim light.

Although this endogenous influence is considerable, the rat's feeding behavior is also sensitive to environmental factors. Partial reversals in the nocturnal feeding pattern were seen when any of the following conditions existed during the light phase: A more palatable diet was provided (Panksepp & Krost, 1975), a small dark box was present in the cage (Vilchez & Echave Llanos, 1971), access to food was restricted to this phase (Spiteri, 1982), or procurement or consumption cost of feeding was low relative to the cost in the dark phase (Jensen, Collier, & Medvin, 1983). Experiment 1 investigated the influence of another environmental factor on nocturnal feeding, namely, the risk of predation. If the rat's foraging behavior is organized so as to reflect the risk of predation, then the rat's strong tendency toward nocturnal feeding may be the most identifiable aspect of its preencounter defensive strategy.

Experiment 1 was designed to examine the effects that presenting shock in association with a phase of the light/dark cycle would have on the rat's foraging behavior. According to the selective association hypothesis, the rat's foraging behavior was expected to undergo greater reorganization if shock was delivered during the light phase than it would if shock was delivered during the dark phase. Thus, decreases in total consumption and meal frequency in the shock-present (S+) phase were expected to be larger for rats exposed to shock during the light than for those exposed during the dark. Also, compensatory increases in total consumption and meal frequency in the shock-free (S-) phase were expected to be larger for rats that had a dark S- phase than for those that had a light S- phase.

Method

Subjects

Twelve female Long-Evans hooded rats were used in this experiment. The rats were born and raised in the Dartmouth College animal colony. Prior to the start of the experiment, the rats were housed individually in standard wire mesh cages (18.5 x 20.5 x 24.9 cm) with Agway Prolab rat chow and water available *ad libitum*. A 14:10 light/dark schedule (lights on at 6:30 a.m., off at 8:30 p.m.) was in effect in the colony room. Two weeks before the start of each replication, four rats were taken in their cages and placed on a table in the laboratory room where a 12:12 light/dark schedule (on at 9:00 a.m., off at 9:00 p.m.) was in effect. Illumination was provided by three fluorescent white lights (two, 34 W, 120 V and one, 56 W, 120 V) during the light phase and by a single 25-W (120-V) red light during the dark phase. Reflected light in

this room was measured at 2.6 footlamberts in the light and .05 footlamberts in the dark. For 10 days before the study began, the experimenter entered the laboratory room at the moment of a change in phase. At these times, the rats were removed from their cages and adapted to handling for approximately 1 min each. Food was removed from the rats' cages 24 h before the animals were placed in the experimental chambers. The rats were approximately 120 days of age at the start of the experiment.

Apparatus

Four identical chambers were used (58.5 x 26 x 20.6 cm). The walls, hinged ceiling, and nest area of each chamber were made of clear acrylic plastic. The bar-press manipulandum was centered on one of the 26-cm side walls at a height of 4 cm above the grid floor. A Scientific Prototype (Model D700) feeder was used to dispense food pellets (45 mg Bioserve) to a recessed cup located 9.5 cm to the left of the bar. A water spout entered the chamber on the same wall, 9 cm to the right of the bar. A 1.1-W (28-V) cue light was located 8 cm directly above the bar in each chamber. From the opposite 26-cm side wall, the nest area extended 16.5 cm toward the center of the chamber and spanned the entire width. This area was filled with wood shavings. Except for the nest area, the floor of each chamber was composed of 25 brass rods (3 mm), spaced 1.6 cm center to center, and daisy-chained together with neon lights. Electric footshock, 1 s duration and approximately 1 mA intensity, could be delivered to the grid floors. In measuring shock intensity, a 39-kohm resistor was substituted for the rat. Voltage (AC) readings were taken between rods at increasing separations, up to 10 rods apart. The shocker was calibrated such that the intensity setting corresponded to the mean of the 10 readings. (See Fanselow & Lester, 1988 for an illustration of the chamber.)

Procedure

Rats were placed in the chambers at the start of the experiment and lived in those chambers throughout the experiment. The rats spent approximately 2 weeks under preshock conditions and 2 weeks under shock conditions. (These periods were extended when equipment failures occurred. Data from the day in which the experiment was disrupted and the subsequent day were not included in any of the analyses.) A chained FR1:CRF schedule was in effect under both the preshock and shock conditions. According to this schedule, a single procurement bar press turned on the cue light that signaled the beginning of a meal. Thereafter, each bar press resulted in the delivery of one food pellet. If 4 min elapsed without a bar press, the cue light went off and the meal was terminated. No shaping of the bar-press response was necessary. Water was freely available at all times. Three independent groups of four rats each were run. For the rats in Group L+/D-, 15 shocks were programmed to occur at random times during the

light phase but none occurred during the dark phase. Rats in Group L-/D+ had the relationship between phase and shock were reversed. For the rats in Group L50/D50, 15 shocks were programmed for random times throughout the 24-h period, with either seven or eight shocks delivered in a given phase. The number of shocks per phase (seven or eight) was determined by the toss of a coin with the restriction that the same number was not delivered for more than three consecutive phases. Shock was programmed to occur independently of the rat's behavior. The rat could avoid shock by remaining in the nest area, but by doing so the rat forfeited access to food and water. The study was run in three replications with groups counterbalanced in terms of chamber assignment and replication. Total consumption, meal frequency, meal size, and body weight data were recorded separately for the light and dark phases. A "meal" was operationalized as any time the rat bar-pressed for at least three food pellets before the cue light went out. The means from the data collected over the last 4 days of the preshock and shock conditions were used in the analyses.

Results and Discussion

The data were analyzed first with respect to absolute change and subsequently with respect to directional change. An *absolute change score* was calculated by adding the absolute value of the change in the light and the absolute value of the change in the dark (e.g., for total consumption: number of pellets decreased during the S+ phase of the light/dark cycle plus number of pellets increased during the S- phase of the light/dark cycle). Thus, this score reflected change independent of direction. The absolute change score was constructed so that the total reorganization (i.e., changes occurring in the S+ phase and compensatory changes occurring in the S- phase) of a consumption variable could be examined in a single analysis that would not be affected by differential sensitivity of light and dark measures. A one-way analysis of variance with a full set of planned comparisons was performed on the absolute change scores for total consumption (see Table 1). The comparisons indicated that rats in Group L+/D- did not differ from rats in the control group (L50/D50) in terms of absolute change in total consumption ($F < 1$). In fact, rats in Group L+/D- showed far less change than did rats in Group L-/D+, $F(1, 9) = 58.9$, $p < .001$, which also differed reliably from the control group, $F(1, 9) = 44.6$, $p < .001$. Thus, the data on total consumption did not provide any support for the hypothesis that nocturnal feeding reflects a selective association between light and aversive stimulation because rats shocked only in the light failed to show the greatest absolute change. On the contrary, shock had the greatest effect on total consumption when it was delivered only during the dark portion of the light/dark cycle.

Similar results were obtained when the data were broken down to reflect absolute change in meal frequency and meal size (see Table 1).

Table 1

Mean Absolute Change Values from the Preshock to Shock Conditions and Mean *Absolute Change Scores* from Experiment 1

	Total Consumption (pellets)		
	absolute change Light Phase	absolute change Dark Phase	*Absolute Change Score*
Group L+/D-	53.1	31.0	84.2
Group L-/D+	173.8	190	363.8
Group L50/D50	35.9	84.5	120.4
	Meal Frequency		
	absolute change Light Phase	absolute change Dark Phase	*Absolute Change Score*
Group L+/D-	2.2	.8	2.9
Group L-/D+	1.8	7.4	9.2
Group L50/D50	1.8	4.9	6.6
	Meal Size (pellets/meal)		
	absolute change Light Phase	absoulte change Dark Phase	*Absolute Change Score*
Group L+/D-	17.6	6.0	23.6
Group L-/D+	45.3	33.9	79.2
Group L50/D50	10.6	12.4	22.9

Note. For each subject the *Absolute Change Score* (ACS) was calculated as follows:

$$ACS = \underbrace{|\text{pre-shock value} - \text{shock value}|}_{\text{Light Phase}} + \underbrace{|\text{pre-shock value} - \text{shock value}|}_{\text{Dark Phase}}.$$

In terms of meal frequency, Group L+/D- was influenced less by shock than was the control group which was administered half as many shocks during the light phase, but was given the remainder of shocks during the dark phase. This difference was marginally reliable, $F(1, 9) = 4.7$, $p < .06$. Once again, the greatest absolute change was noted for rats that received all shocks during the dark phase. Group L-/D+ showed reliably more change in meal frequency than did Group L+/D-, $F(1, 9) = 13.7$, $p < .01$, and did not differ from Group L50/D50, $F(1, 9) = 2.3$, $p < .2$. In terms of meal size, the mean absolute change score for Group L+/D- was significantly less than that for Group L-/D+, $F(1, 9) = 17.9$, $p < .005$, and was virtually equal to that of Group L50/D50 ($F < 1$). In sum, none of the three indices of foraging behavior offered support for the idea that nocturnal feeding in the rat reflects a selective association between aversive events and light. To the contrary, changes in consummatory behavior brought about by shock were always greatest when shock was delivered exclusively during the dark.

The absolute change scores used in the above analyses were calculated in a manner that was conservative in the direction of the predicted effects. That is, change was described as a simple difference measure rather than a percentage change because this method minimized change in the light phase where the numbers tended to be small and maximized change in the dark phase where the numbers tended to be large. Given the consistently large changes noted for

Group L-/D+, the absolute change scores were recalculated on a percentage basis and the analyses repeated to determine if the observed outcomes would hold up when change was minimized in the dark phase. The observed outcomes did indeed hold up. The only deviation in statistical significance was noted in the analysis of the data on meal frequency. Previously, a marginally significant difference was reported for the comparison between Group L+/D- and Group L50/D50. In the reanalysis, the order of the groups was the same, but the difference between Group L+/D- with the smallest mean absolute change score and the control group with an intermediate mean absolute change score did not approach significance, $F(1, 9) = 1.7$, $p < .3$.

To gain a better understanding of the large and unexpected changes that were found for Group L-/D+, a series of exploratory analyses of variance were conducted with post hoc comparisons made by the Newman-Keuls method ($p < .05$). Light and dark phase data were examined in separate analyses to avoid the problem of differential sensitivity in the dark phase dependent measures. The data from the analyses on total consumption are shown in Figure 1. Group L+/D- and Group L-/D+ each showed significant reductions (53.1 pellets or 84% and 190 pellets or 87.3% respectively) in total consumption during their S+ phase of the light/dark cycle. The most notable aspect of this set of analyses was the large increase (173.8 pellets or 177.5 %) in consumption during the light phase (S-) when Group L-/D+ was exposed to shock. This compensatory increase accounted for the fact that Group L-/D+ differed from each of the other groups. No such compensatory effect was seen during the dark phase (S-) for Group L+/D-. Between group differences in the dark phase were the result of varying decrements in consumption as a result of shock. Thus, all three groups differed from each other: Group L+/D- consumed the most and was not given any shocks, Group L50/D50 consumed an intermediate amount and was given an intermediate number of shocks, and Group L-/D+ consumed the least and was given the largest number of shocks.

Figure 2 displays the data in terms of meal frequency. Within group comparisons were not made for the light phase data because the Shock Condition x Group interaction was not reliable. However, between group comparisons indicated that the group that was not shocked during this phase (Group L-/D+) took more meals than either of the other two groups. The dark phase data showed that shock had a large effect on meal frequency for Group L-/D+ (decrease of 7.4 meals or 93.3%). Group L50/D50 also showed a significant reduction (4.9 meals or 49.6%) in meals taken in the dark phase during the shock condition. In the dark phase, Group L-/D+ took fewer meals than either of the other groups.

In previous research (Fanselow & Lester, 1988; Fanselow et al., 1988) it was noted that when the cost of procuring a meal was set at 32 bar presses, the rat reduced the time it spent at risk of shock by procuring fewer, but larger meals. Because the cost of procuring a meal was set very low (FR1) in the present experiment, the difference in time

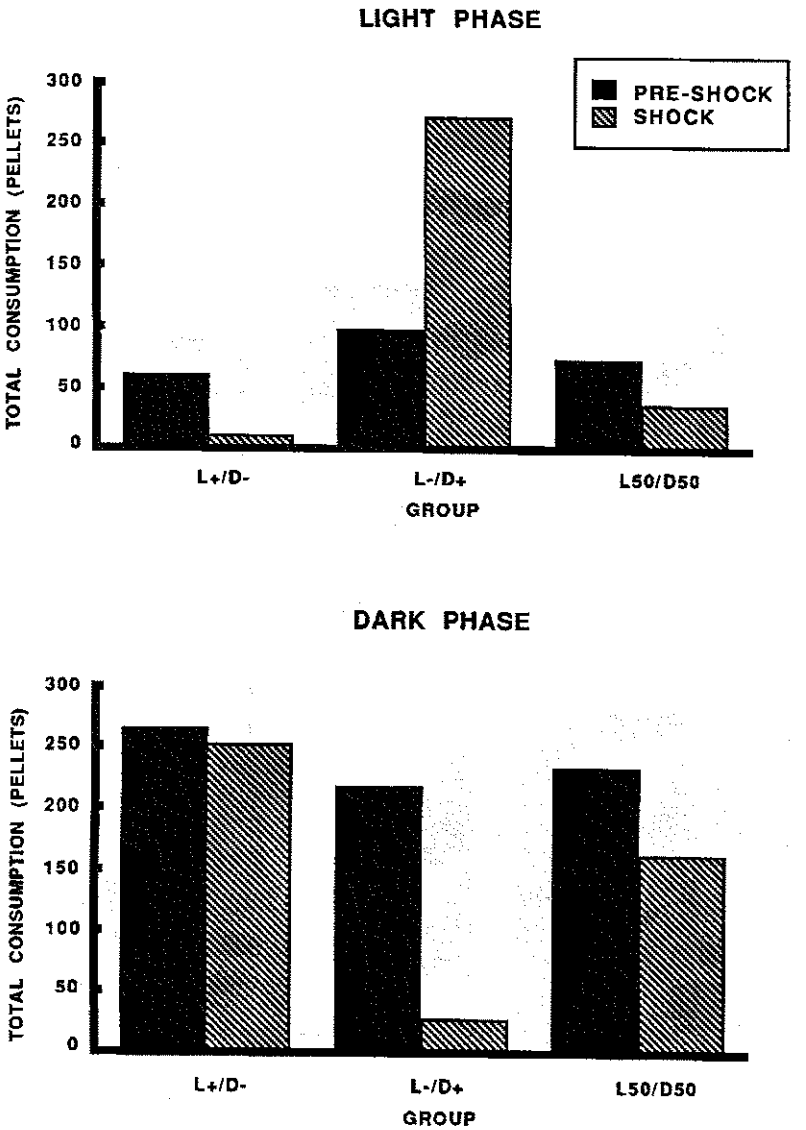

Figure 1. The data from Experiment 1 displayed in terms of total consumption during the light phase (top) and dark phase (bottom). Within each phase, total consumption is broken down by group and shock condition.

at risk was minimal whether the rat procured many small meals or just a couple large meals. Therefore, large changes in meal size as a function of shock were not expected. As can be seen in Figure 3, the only reliable change in meal size was an increase in meal size that occurred during the light phase for Group L-/D+. In other words, this change appeared as

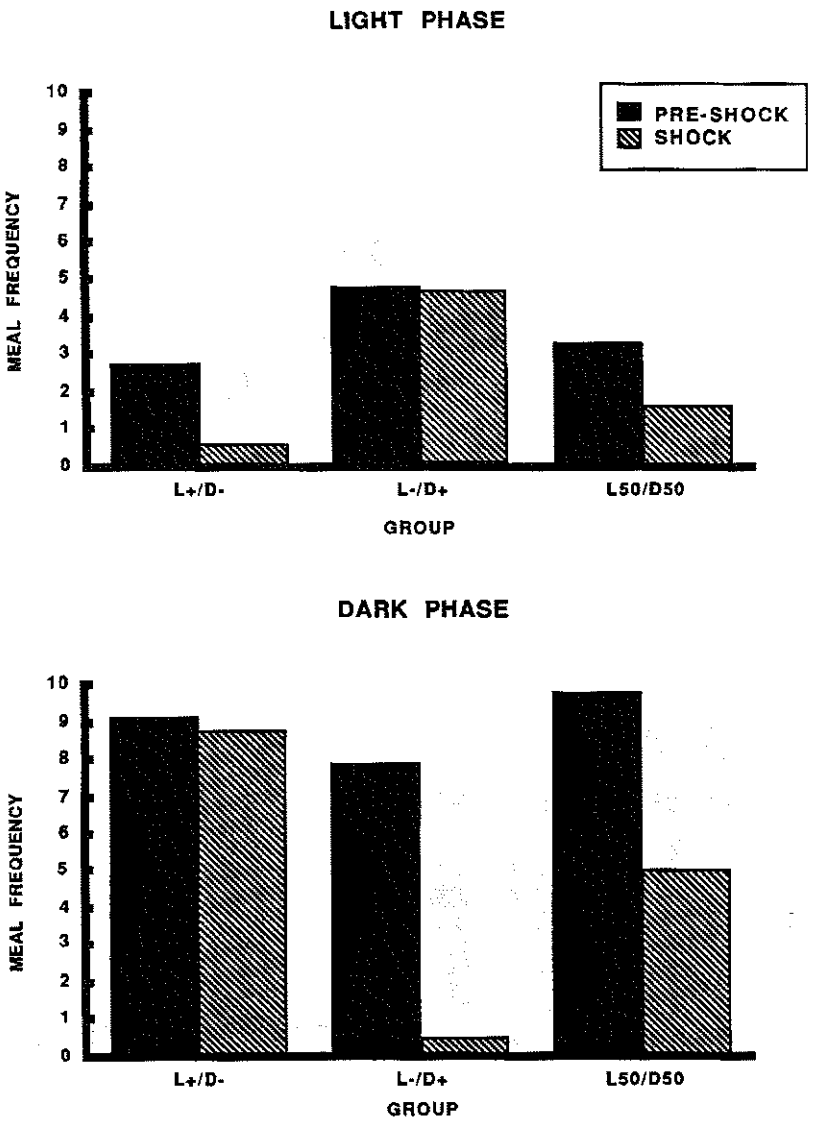

Figure 2. Meal frequency in the light phase (top) and dark phase (bottom) as a function of group and shock condition.

a large compensatory increase (45.3 pellets/meal or 197.5%) during the S- phase and accounted for the fact that Group L-/D+ took larger meals than the other two groups. The finding of no overall increase in average meal size when shock was introduced on an FR1:CRF is quite consistent with our earlier report that meal size increases were much greater on FR90:CRF than FR10:CRF (Fanselow et al., 1988).

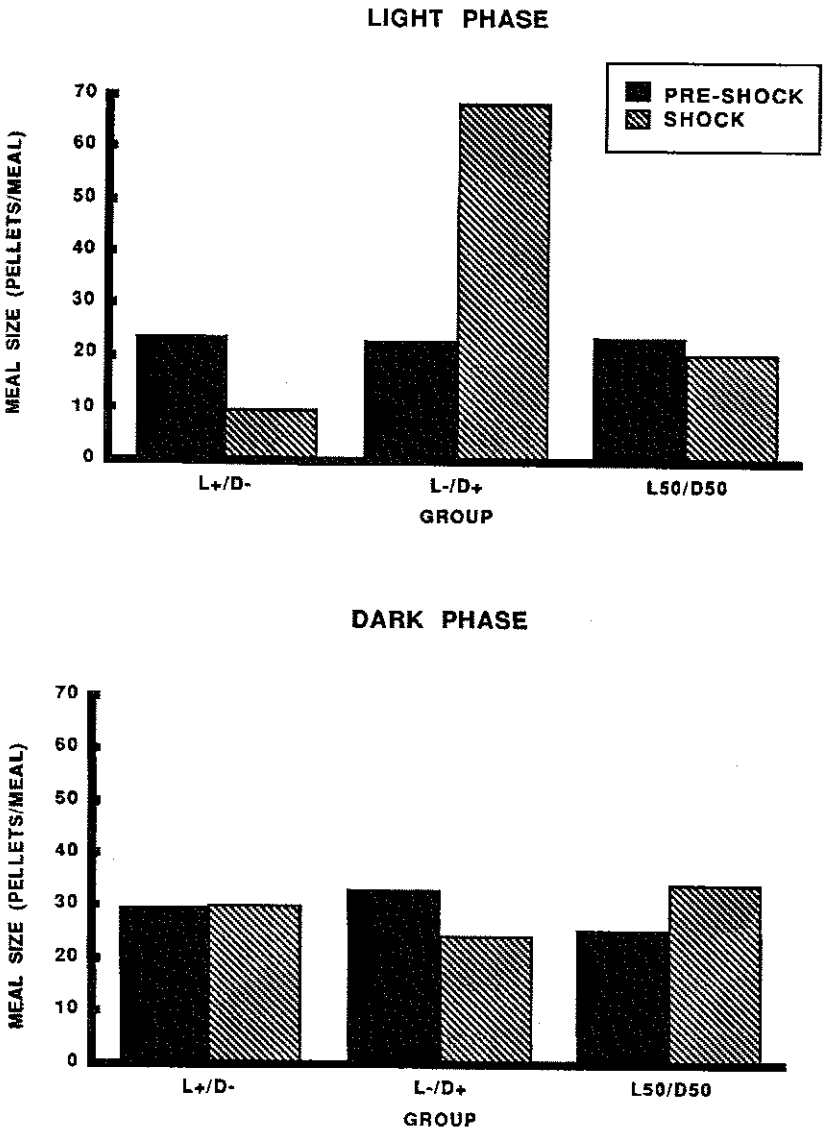

Figure 3. The meal size data are shown here for the light phase (top) and dark phase (bottom) as a function of group and shock condition.

To verify that the changes noted during the shock condition represented conditioned effects, the rat's meal-taking behavior prior to the first shock of the day was examined. Presumably, if the rats had learned the phase-shock association, they would not bar press during

the S+ phase, even before shock actually occurred. Alternatively, if the rat's meal taking was suppressed each day as a consequence of receiving shock, bar presses would be likely before shock delivery. Also, rats that had learned the phase-shock relation were expected to bar press early in the S- phase (i.e., prior to the delivery of shock to rats then in their S+ phase). The percentage of the last four shock days on which bar presses were made before shock delivery was determined for each rat, for each phase. In a rat's S- phase, the time of the first shock delivered to rats then in their S+ phase was used as the cutoff. The data were subjected to a 3 x 2 analysis of variance with shock group and phase of the light/dark cycle as factors. The Group x Phase interaction was reliable, $F(2, 9) = 24.3$, $p < .001$. Once again, the Newman-Keuls method ($p < .05$) was used to make comparisons between the S+ and S- phase means for each group. These comparisons indicated that by the end of the shock phase, the rat's feeding behavior was under stimulus control. The rats in Group L+/D- never bar pressed before shock in the light phase but, on the average, did so in the dark phase 87.5% of the time. Conversely, Group L-/D+ rats never bar pressed before shock in the dark phase but did so in the light phase 68.8% of the time. Rats in the control group bar pressed before shock in the dark phase more often (56%) than they did in the light phase (6.2%).

Taken together, these exploratory analyses indicated that the rats did learn to associate shock with the phase of the light/dark cycle with which it was paired. The large decrement in total consumption observed for Group L-/D+ during its S+ phase was caused primarily by a drop in meal frequency. Also, it was discovered that the compensatory increase in consumption seen during the S- phase was the result of an increase in meal size. Analysis of the body weight data indicated that although there was a trend toward weight loss in the shock condition (mean preshock body weight = 281.8 g, mean shock body weight = 273.6 g), neither the main effects nor interactions were reliable.

The results of this first experiment indicated again that foraging behavior in the rat is sensitive to the risk of predation (Fanselow & Lester, 1988; Fanselow et al., 1988). Rats in Group L+/D- and Group L-/D+ reorganized their meal taking and reduced the time spent feeding during the S+ phase. However, the finding that the largest changes in the rat's foraging behavior occurred when shock was delivered exclusively during the dark phase did not support the hypothesis that nocturnal feeding in the rat is a preencounter defensive behavior. Similarly, the data were not indicative of a selective association between light and aversive events. These data should not be taken as evidence that rats are unable to suppress further the infrequent meals taken during the light phase. Jensen et al. (1983) found that with phase dependent increases in the lever press requirement, rats switched to feeding exclusively in the dark sooner than they switched to feeding exclusively in the light.

In this first experiment, it may have been the case that rats in Group L-/D+ showed the greatest changes in foraging because they received

the largest number of shocks. Unfortunately, the apparatus was not equipped to record the rat's location (either safe in the nest area or at risk on the shock grids) at the time of shock delivery. However, at least on the first day of the shock condition, the probability of the rat's being shocked was greater if shock was paired with the dark phase (the phase when the animal had previously spent a relatively large portion of time taking meals out on the gridded area) than if shock was paired with the light phase (the phase when the animal had probably spent a relatively large amount of its time asleep in the nest area). Although this possibility of greater shock exposure during the dark phase worked against the hypothesis of selective association between light and shock, it may have contributed to the observed results. However, analyses of the data collected from Group L+/D- during the shock condition indicated that the outcome of this experiment probably would not have differed if rats in this group had received additional shocks (i.e., as many as rats in Group L-/D+). The data on total consumption, meal frequency, and meal size were entered in separate analyses of variance with Phase and Days as repeated measure factors. The Days factor had five levels: a block of the first two days of the shock condition and four blocks of two days each from the last 8 days of the shock condition. Each of the three analyses yielded reliable phase effects, for all Fs(1, 3), $p < .05$, indicating that the rats consumed more and larger meals during the shock-free dark phase. However, no reliable effects were found for the Days factor or its interaction with Phase, all Fs(4, 12) ≤ 1. In other words, each of the dependent measures had reached asymptotic levels by the end of the shock condition. Therefore, additional experience with shock would not have been expected to change levels of responding.

Experiment 2 was designed as a further test of the selective association hypothesis. This time, the hypothesis was tested in a situation where the postencounter defensive behavior, freezing was the behavior under observation and shock exposure in the light and dark was equated.

Experiment 2

A considerable amount of research has been done that compares the associative properties of light/dark CSs with those of auditory CSs. These studies have typically pointed to two findings. First, although comparable levels of context conditioning occur when either a light or white noise CS is present before shock, less conditioned fear is elicited by the CS itself when it is a light than when it is a noise (Sigmundi & Bolles, 1983; Sigmundi, Bouton, & Bolles, 1980; Van Willigen, Emmett, Cote, & Ayres, 1987). Second, although the onset of light or dark serves as a better safety signal than does white noise, the reverse is true when these stimuli are used as warning signals (Jacobs & LoLordo, 1977; 1980). These studies have not compared directly the effectiveness of aversive conditioning using a light CS versus that using a dark CS.

Of greater relevance to the present research is a study conducted by

Welker and Wheatley (1977). They used a conditioned suppression procedure and found evidence of selective association between light/dark CSs and shock. They reported that suppression of bar pressing was reliably greater when the CS signaling the occurrence of shock was an increase in luminance than when the CS was a decrease in luminance. Suppression of bar pressing in a CER procedure reflects an increase in the postencounter defensive behavior referred to as freezing (Bouton & Bolles, 1980). Experiment 2 used the differential conditioning procedure and a design that allowed direct observation of the freezing response. Light and dark phase control groups not present in the conditioned suppression research were included in this study. These additional control groups made it possible to separate the effects of chamber light/dark CSs from those of light/dark phase CSs. If light is selectively associated with aversive stimulation, it would be expected that the groups that received shock paired with light would show faster rates of conditioning and/or differentiation of the freezing response relative to groups that received shock paired with dark.

Method

Subjects

The 24 female Long-Evans hooded rats used in this experiment were bred and raised in the Dartmouth College animal colony under the same conditions described for rats in Experiment 1. Three weeks before the start of the experiment, the entire rack of animals was relocated to a room separate from the colony room. There, the rats were allowed to adapt to the 12:12 light/dark schedule (on at 7:00 a.m., off at 7:00 p.m.) and were exposed to the same handling procedure used in Experiment 1. The room was illuminated by two fluorescent white lights (one 35 W, 120 V and one 56 W, 120 V) during the light phase and by a single 25-W (120-V) red light during the dark phase. Reflected light was measured at 4.2 footlamberts in the light and .06 footlamberts in the dark. Food and water were freely available at all times. The rats ranged in age from 104-125 days of age at the start of the experiment.

Apparatus

Four identical observation chambers (23.5 x 29 x 19.5 cm) were used. The 29-cm side walls were made of stainless steel. A recessed food cup was located on one of the side walls within each chamber, but it was not used. The front and back walls and the ceilings were made of clear acrylic plastic. The floor of each chamber was composed of 18 stainless steel rods (2.5 mm), spaced 1.25 cm center to center, and wired to a Grason-Stadler (Model 700) shock generator/scrambler. Each observation chamber was situated within its own sound- and light-attenuating chest such that it was visible through the 30- x 30-cm clear plastic window in the front of the chest. Illumination was provided by a 7.5-W (120-V) white or red light mounted on the ceiling of each chest

(12.5 cm above the observation chamber's ceiling). Reflected light in the chambers was measured at 1.1 footlamberts with the white light and .13 footlamberts with the red light. Ventilation fans provided background noise at 73 dB (C scale).

Procedure

On the first two days of the experiment, rats were taken to the laboratory room where they received two 4.5-min exposures (15 min apart) to one of the four observation chambers. The chambers were illuminated during one exposure and darkened (except for the red light) during the other. These adaptation periods were shock free. On subsequent days, the rats continued to receive two 4.5-min placements in the same chambers, but 4 min into one of these periods a .4-mA, .5-s shock was delivered through the grid floors. For one third of the rats, shock was delivered only when the chamber was illuminated (L+/D-). Another third of the rats received shock when in the darkened chamber (L-/D+), and the remaining rats received shock 50% of the time under each lighting condition (L50/D50) according to a randomized block design.

A rat's tendency to freeze in a light/dark chamber might be different from its tendency to freeze in that chamber when actually in the light/dark phase of its cycle. Therefore, half the rats from each of the three conditions were run during their light phase (start 2.5 h into light phase) and half were run during their dark phase (start 2.5 h into dark phase). Rats run during their dark phase were kept in constant darkness except for the 4.5-min exposure to the light chamber. This brief exposure to light should not have been long enough to reset the rat's circadian rhythm (Aschoff, Hoffmann, Pohl, & Wever, 1975). Thus, the 24 rats were divided into six groups of four rats each. Order of exposure to the light and dark chamber was counterbalanced between subjects within a day and within subjects over days. Also, half the rats in Group L50/D50 first received shock in an illuminated chamber whereas the other half first received shock in a darkened chamber.

Five shock-free test days were included in this study. These days occurred on the day after Conditioning Days 2, 4, 6, 8, and 24. On these days, half the rats from each of the six groups received the two placements in the chambers (once illuminated, once darkened) during the light phase. The rest of the rats were exposed similarly to the chambers during the dark phase. During these shock-free test days, the experimenter and a co-observer were blind to the rats' group assignments.

On all days of the experiment, a time sampling procedure (e.g., Fanselow & Bolles, 1979) was used to record the following classes of behavior over the first 4 min of each exposure: (1) *freezing* - the absence of all visible movement of the body and vibrissae except for movement necessitated by breathing, (2) *grooming* - any scratching, licking, or rubbing by the rat of its own body, (3) *rearing* - lifting of the two

front paws off the floor, (4) *locomotion* - use of the rear legs in forward motion, and (5) *general activity* - all other behaviors were scored in this category. The observer scanned from one rat to the next at a 2-s pace, returning to the same rat every 8 s. Previous checks using this scoring method have indicated high interobserver reliability (90 - 99%). The observation chambers were cleaned between rats with a 5% solution of ammonium hydroxide and tap water.

Results and Discussion

The percentage of behavior samples scored as freezing was determined for each rat for each day of the experiment. The freezing scores from the conditioning days were subjected to a 3 x 2 x 2 x 12 analysis of variance. The factors in this analysis were the shock group the rat was assigned to, whether the chamber was light or dark, whether the rat was run during the light or dark phase, and the blocks of 2 conditioning days. Because the freezing scores for the rats run during the light phase did not differ from those of rats run during the dark phase, the data were collapsed over the Phase factor for illustration in Figure 4. The main effect for Days was reliable, $F(11, 198) = 16.7$, $p < .001$, with the percentage of samples scored as freezing increasing over conditioning days. The main effect for Chamber was also reliable, $F(1, 18) = 32.6$, $p < .001$. The mean percentage of freezing in the light chamber was 38.9 and that in the dark chamber was 46.5. The Group x Chamber x Days interaction was also significant, $F(22, 198) = 2.1$, $p < .005$. However, it is apparent from Figure 4 that the form of this interaction did not lend support to the hypothesis that rats selectively associate light with aversive events. This impression was confirmed in a series of five planned comparisons of the freezing scores from the last block of 2 conditioning days. These comparisons were made with alpha adjusted to hold the overall possibility of a Type I error at $p < .05$. Rats that had shock paired with the light chamber (Group L+/D-) did not freeze any more in the light chamber than they did in the dark chamber. This was also true of rats in the control group (Group L50/D50). Only the rats that had shock paired with the dark chamber (Group L-/D+) learned the discrimination as evidenced by reliably more freezing in the dark chamber than in the light chamber. A comparison between the S+ condition for Group L+/D- and that for Group L-/D+ also showed reliably more freezing to the dark S+ than to the light S+. The two groups did not differ in terms of freezing to S-.

The freezing scores from each of the 5 test days were subjected to separate analyses similar to that described for the conditioning data. Since the experimenter and co-observer had high interobserver reliability ($r = .97$) and the Observer factor did not interact with the other variables (Group, Chamber, and Phase) when included as a repeated measure in the analysis of variance, only the experimenter's observations are described here. A reliable main effect for Chamber was found on the

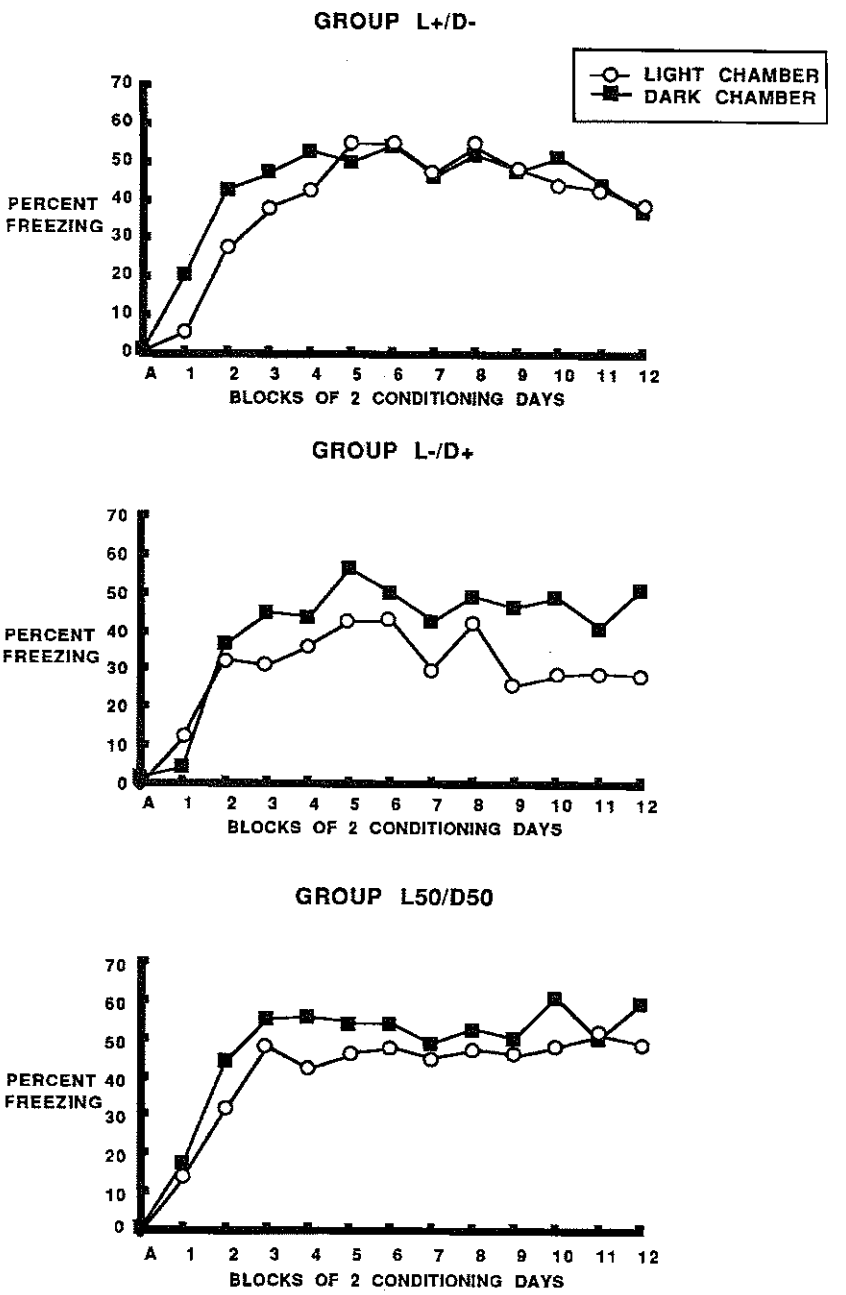

Figure 4. The percentage of time samples scored as freezing in Experiment 2. The data are shown for the three shock groups in terms of chamber illumination and blocks of 2 conditioning days.

first, $F(1, 18) = 6.4$, $p < .05$, and second, $F(1, 18) = 6.97$, $p < .05$, test days, with rats freezing more in the dark chamber than in the light chamber. A reliable Chamber x Phase interaction was also present on the second test day, $F(1, 18) = 8.6$, $p < .01$. Rats run during the light phase engaged in more freezing in the dark chamber than in the light chamber. Freezing scores for rats run during the dark phase did not differ for the two chambers. No reliable effects were found on the third, fourth, or fifth test days. The Group x Chamber interaction did not hold up on any of the test days. Group L-/D+'s ability to discriminate between the two chambers may not have been sufficiently strong to show up in a single day's worth of data or may have been disrupted for rats that were run 12 h earlier/later than usual.

The findings from the conditioning data are consistent with those of Experiment 1 and do not suggest that associations are more easily formed between light and shock than between dark and shock. However, the exploratory analyses from the first experiment indicated that when shock was paired with the light phase (Group L+/D-), the rats did learn the association as evidenced by a reliable reduction in total consumption during that phase. The present experiment found that when shock was paired with a light chamber and freezing was the dependent measure, the rats in Group L+/D- did not show any indication of having learned the association (i.e., they did not show any more freezing in the light chamber than in the dark chamber). In both experiments, shock produced the greatest measurable effects on behavior when delivered reliably in the dark.

Experiment 3

The results of Experiment 2 indicated that, in terms of differential freezing in the S+ and S- chambers, rats were able to learn the association between shock and a dark chamber, but not that between shock and a light chamber. The third experiment was designed to assess the possibility that rats could learn an association involving the light chamber if the light chamber provided information about food rather than shock and a discriminatory response other than freezing was required. If rats in the present experiment are able to learn the association between the light chamber and food, it suggests that rats in this and the previous experiment were making associations in a selective manner (i.e., relating some CSs and USs and not others). Alternatively, if Group L-/D+ acquires the discrimination and Group L+/D- fails to do so again, it suggests that the rat is simply unable to use the light chamber as a CS irrespective of the particular US it is paired with or the discriminatory response that is required. If this is the case, it indicates that the light condition (or the light condition relative to the dark condition) used in Experiment 2 and the present experiment differed in some important way from that used in Experiment 1.

Method

Subjects

The subjects used were six Long-Evans hooded rats approximately 100 days of age at the start of the experiment. The rats were given the same preexperiment care as described for those used in Experiment 2 with the exception that these rats were reduced to 80-85% of their *ad libitum* weight during the week before the experiment began. The rats were maintained at this weight throughout the experiment.

Apparatus

One of the chambers described for Experiment 2 was used in this experiment, although the shocker was never turned on.

Procedure

The six rats were randomly divided into two groups. For rats in Group L+/D-, a 45-mg Noise food pellet was placed in the food cup on trials when the chamber was illuminated (S+). The food cup was empty on trials when the chamber was darkened (S-). S+ and S- conditions were reversed for rats in Group L-/D+. On the first day of the experiment, each rat was given a single S+ trial followed by a single S- trial. On the S+ trial, the rat was given unlimited time to find and consume the pellet of food. Based on these times, a 2-min cutoff latency was established. On each of 14 conditioning days that followed, the rats were given two exposures to the S+ condition and two exposures to the S- condition. The sequence of lighting conditions (light-L or dark-D) across the four trials was either LDDL or DLLD and was alternated daily. For half the rats in each group the first trial was an S+ trial. For the other half, the first trial was an S- trial. Each of the rats received its first trial and was returned to a holding cage. At 20, 40, and 60 min after the start of the procedure, the experimenter began the second, third, and fourth trials respectively.

Results and Discussion

The latency values were subjected to a reciprocal transformation (Edwards, 1972) and were then entered in a 2 x 2 x 7 analysis of variance. The factors in the analysis were the group the rat was assigned to, whether the chamber was light or dark, and the blocks of 2 conditioning days. The data are displayed in Figure 5. The analysis confirmed the apparent main effects for Days, $F(6, 24) = 4.4$, $p < .005$, and Chamber, $F(1, 4) = 17.2$, $p < .05$. Rats entered the food cup more quickly as the experiment progressed and tended to enter the food cup more quickly in the dark chamber than in the light chamber. The reliable Group x Chamber interaction, $F(1, 4) = 40.7$, $p < .005$, was examined using a set of four planned comparisons with the data from the last block of 2 conditioning days. A Bonferroni correction was used to hold the

overall possibility of a Type I error at $p < .05$. As in the previous experiment, the reliable interaction with the Group factor was indicative of Group L-/D+ learning the discrimination and Group L+/D- failing to do so. Thus, rats in Group L-/D+ entered the food cup more quickly when the chamber was dark than when it was light, and rats in Group L+/D- did not differ in the time it took to enter the food cup under the two conditions. The comparison between each of the group's S+ conditions established that rats were faster under the dark S+ than under the light S+. The two groups did not differ in terms of latency to enter the food cup in their S- conditions.

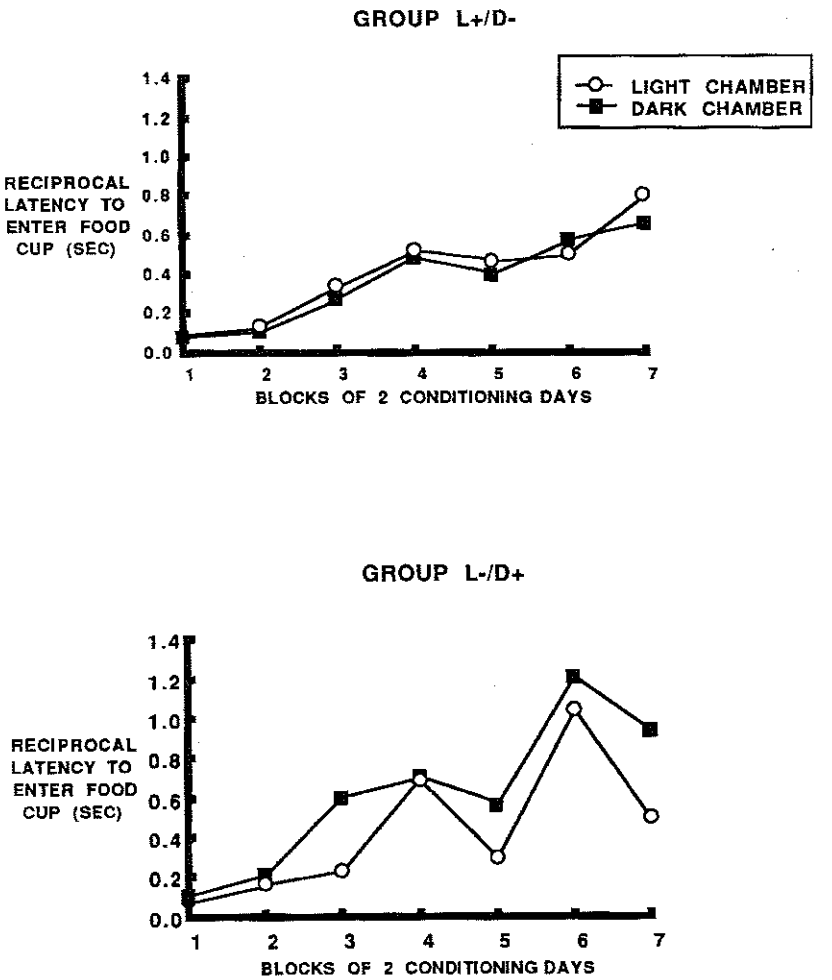

Figure 5. The reciprocal latency data from Experiment 3. The data are shown for Group L+/D- (top) and Group L-/D+ (bottom) as a function of chamber illumination and blocks of 2 conditioning days.

Taken together, the results of Experiments 2 and 3 indicated that rats were unable to acquire a discrimination between a light and dark chamber when the light chamber was paired with either an appetitive or aversive US. Although the phase CSs (Experiment 1) and the chamber CSs (Experiments 2 and 3) were not equated in terms of reflected light, the results of these experiments with chamber CSs are suggestive of the possibility that light per se was not the aspect of the CS that allowed Group L+/D- to acquire the discrimination in Experiment 1.

Experiment 4

This experiment again employed the differential conditioning procedure to examine the possibility of selective association between light and aversive stimulation. As in Experiment 2, the postencounter defensive behavior freezing was observed. However, this time the light and dark CSs were the phases of the light/dark cycle. If, as suggested by the results of the first three experiments, the phase CSs provide the rat with information other than light/dark per se, Group L+/D- might acquire the discrimination in this experiment even though it was unable to do so in Experiment 2.

Method

Subjects

The 24 female Long-Evans hooded rats used in this experiment had been exposed to the same conditions as described for rats in Experiment 2, although these animals were housed in the room with the 12:12 light/dark cycle for 6 weeks prior to the start of the experiment. The rats were all about 110 days of age on the first day of the experiment.

Apparatus

The same four chambers described in Experiment 2 were used in the present experiment.

Procedure

The procedure used in Experiment 2 was followed as closely as possible. The only major change in the design was that shock was paired with the light and/or dark phase rather than the light and/or dark chamber. This caused the two exposures to the chambers to be separated by approximately 12 h, rather than 15 min as in Experiment 2. Light phase trials began 1 h into the light phase, dark phase trials began 1 h into the dark phase. Half the rats received both exposures in a light chamber and the other half received both exposures in a darkened chamber. The four shock-free test days included in this study occurred on the day after Conditioning Days 3, 5, 7, and 9. On these days, the rats' chamber condition (light or dark) was maintained but the observer and co-observer were blind to the rats' shock group assignments.

Results and Discussion

As in Experiment 2, the raw data were converted to the percentage of samples scored as freezing. A 3 x 2 x 2 x 7 analysis of variance was performed on the freezing scores from the conditioning days. The factors in the analysis were the shock group the rat was assigned to, whether the phase was light or dark, whether the rat was exposed to a light or dark chamber, and the blocks of 2 conditioning days. The freezing scores did not differ as a function of whether the rat was exposed to a light or dark chamber. Therefore, the data were collapsed over the Chamber factor for illustration in Figure 6. As usual, the main effect for Days was reliable, $F(6, 108) = 18.6$, $p < .001$, with freezing increasing over conditioning days. The main effect for Phase was also reliable, $F(1, 18) = 7.9$, $p < .05$, with rats freezing about 14% of the time during light phase exposures and about 17% of the time during dark phase exposures. A set of five planned comparisons was made within the Group x Phase x Days interaction, $F(12, 108) = 4.6$, $p < .001$, to test the predictions made from the selective association hypothesis. These comparisons were made with alpha adjusted to hold the possibility of a Type I error at $p < .05$ for the set. Comparisons between the freezing scores on the last block of 2 conditioning days indicated that Groups L+/D- and L-/D+ both acquired the discrimination. This was evidenced by reliably more freezing in the S+ phase than in the S- phase. The control group (Group L50/D50) showed very similar levels of freezing in the light and dark phases. Although Groups L+/D- and L-/D+ did not differ in terms of the level of freezing supported by the S+ condition, the groups did differ in terms of rate of differentiation. As shown in Figure 6, the levels of freezing in the light and dark phases began to separate in the appropriate directions after just a few conditioning days for Group L-/D+, but required 7 or 8 days for Group L+/D-. A series of post hoc comparisons (Newman-Keuls, $p < .05$) made on the means from the third block of conditioning days showed that rats in Group L-/D+ were already freezing more in the S+ condition than in the S- condition. At that point, rats in Group L+/D- were still freezing to both S+ and S-, as were rats in the control group (i.e., the differences between S+ and S- freezing scores were not reliable for these groups).

A separate Group x Phase x Chamber analysis of variance was performed on the freezing scores from each of the four test days. Once again, the experimenter and co-observer had high interobserver reliability ($r = .97$) and the Observer factor did not interact with the other variables when included as a repeated measure in the analysis. Therefore, only the experimenter's observations are described here. A reliable main effect for Phase, $F(1, 18) = 9.2$, $p < .01$, was noted on the second test day, with rats freezing more in the dark phase than in the light phase. On the the fourth test day, rats exposed to the light chamber tended to freeze more in the dark phase than in the light phase. This was indicated by a reliable Phase x Chamber interaction on that day,

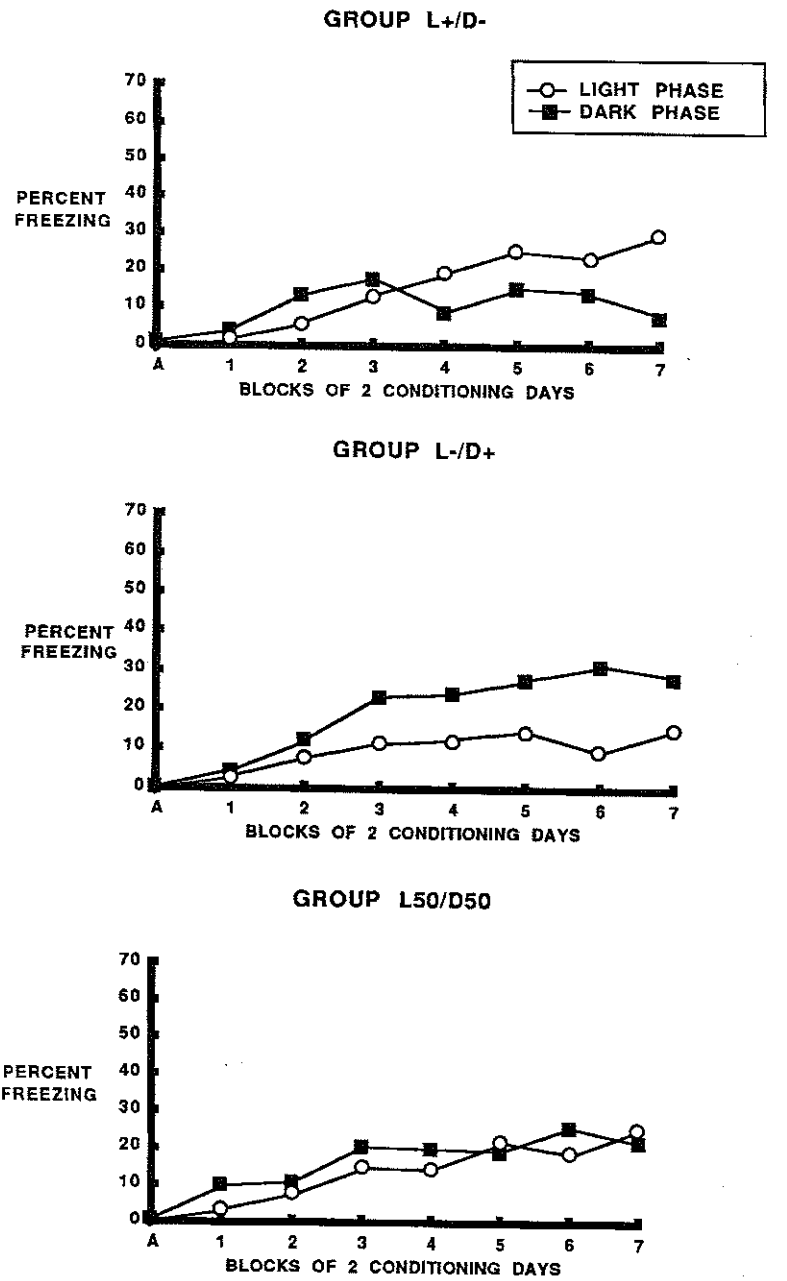

Figure 6. The results of Experiment 4 are shown here as the percentage of time samples scored as freezing. For each of the three shock groups, the data are plotted in terms of the phase of the light/dark cycle and the blocks of conditioning days.

$F(1, 18) = 5.0$, $p < .05$. The Group x Phase interaction was reliable on all four test days, all Fs(2, 18) significant at $p < .01$. The nature of this interaction varied over test days. On the first and third test days, the interaction reflected successful discrimination on the part of Group L+/D-. On the second and fourth test days, only Group L-/D+ showed evidence of having acquired the discrimination. These comparisons were made as sets of three planned comparisons with alpha adjusted as before.

The results of this experiment indicated that rats discriminated between the S+ and S- conditions when shock was paired with either a light or dark phase CS. As in the previous experiments, no evidence for selective association between light and aversive stimulation was found. In fact, rats that had shock paired with the dark phase differentiated between S+ and S- sooner than did rats that had shock paired with the light phase.

General Discussion

The results reported here were consistent across experiments and did not suggest that the rat forms selective associations between light and aversive events. On the contrary, when the effects of shock were measured in terms of changes in foraging behavior (Experiment 1), the greatest reorganization of behavior occurred when shock was paired with darkness. Similarly, when freezing was used as the discriminative response in a differential conditioning study (Experiment 4), the fastest rate of differentiation occurred when shock was paired with the dark phase. Even when the rats failed to show differential freezing in a light S+ chamber and a dark S- chamber (Experiment 2), they did differentiate when the S+ and S- conditions were reversed.

The finding that rats had greater difficulty associating a light CS with a shock US relative to a dark CS and a shock US is inconsistent with the predictions of selective association based on functional considerations that were advanced at the outset. This finding also seems to conflict with Welker and Wheatley's (1977) report that, following pairings of an increase/decrease in illumination with shock, the increase in illumination suppressed food-reinforced lever pressing reliably more than did the decrease in illumination. However, the results of the present experiments are in agreement with the work of other researchers who have noted similar problems when using light and dark cues as predictors of shock. For example, LoLordo and Jacobs (1983) reported that even after repeated pairings of an increase in illumination with shock presentation, the light CS failed to evoke conditioned fear as indexed by an increase in a wheel-running avoidance response. Others (Sigmundi & Bolles, 1983; Sigmundi et al., 1980; Van Willigen et al., 1987) have reported that less conditioned freezing was elicited by a light CS than by a tone CS. In another study, R. A. Sigmundi (personal communication, May 1, 1986) observed freezing in a context that had previously been paired with shock and noted that changing only the lighting condition was not

effective in reducing the contextual fear and freezing. This finding was somewhat surprising in view of the fact that the context shift manipulation has usually been very successful in reducing conditioned fear and freezing (Fanselow, 1980, 1981). However, successful context shift manipulations typically involved changes in more than one stimulus modality. So, for example, Fanselow's (1981) conditioning and test chambers differed in terms of auditory, olfactory, and tactile cues, as well as visual (illumination) cues. One practical implication of the findings reported here is that studies that include context shifts to demonstrate the conditioned nature of behaviors observed in the shock apparatus need not include and should not rely on changes in illumination.

Although the results reported here indicated greater changes in foraging behavior (Experiment 1) and successful discrimination (Experiment 2) or more rapid differentiation (Experiment 4) when darkness rather than light was paired with shock, these findings do not seem to demonstrate a selective association between darkness and aversive events because results of the same nature were found when a light or dark chamber was paired with an appetitive US (Experiment 3). Rats in Group L-/D+ learned the discrimination, but rats in Group L+/D- failed to do so. Thus, rats generally did better when a dark CS was used as the S+ condition, independent of the hedonic qualities of the US that followed. The findings of the present research are also unaccounted for in terms of the relative salience of the light and dark CSs. If the dark CSs were simply more salient to the rat than the light CSs, it would be expected that rats in each of the three groups (L+/D-, L-/D+, and L50/D50) would respond to this difference. In particular, the dark CSs should have been just as noticeable when they were not paired with shock or food (Group L+/D-) as when they were paired with shock or food (Group L-/D+).

These findings are reminiscent of the asymmetry in discrimination learning that occurs when the S+ and S- conditions differ in terms of a single distinctive feature (e.g., a white response key with a small green circle versus a white response key (Hearst & Jenkins, 1974)). Hearst and Jenkins described a "feature positive" arrangement as one in which the stimulus containing the distinctive feature is used as the S+ condition. The stimulus arrangement is referred to as "feature negative" if the distinctive element appears in the S- condition. Using a wide variety of stimuli, these researchers have found that although discrimination proceeds rapidly with the feature positive arrangement, discrimination is slow or unsuccessful with the feature negative arrangement (Hearst & Jenkins, 1974; Jenkins, 1973). Their work with pigeons has indicated that with the feature negative arrangement, the birds continue to respond to the portion of the S- stimulus that is also present in the S+ stimulus (e.g., the white portion of the response key). In the present research, it may have been the case that the light and dark CSs differed in terms of a distinctive feature contained in the dark stimulus. This would account for the finding that performance by Group

L-/D+ (feature positive arrangement) was always superior to that by Group L+/D- (feature negative arrangement).

There is another plausible explanation for the consistently superior performance with a dark CS as the S+ condition. This explanation comes from the studies known as appetitive-aversive interaction experiments (Dickinson & Pearce, 1977). In this kind of experiment, the CS is first paired with a US of one hedonic value and is then examined for its associability with a US of the opposite hedonic value. It seems clear that pairing a CS with an aversive US disrupts subsequent conditioning with that CS and an appetitive US (e.g., Scavio, 1974). The effects of prior appetitive conditioning upon aversive conditioning are not entirely consistent across experiments (e.g., Goodkin, 1976), yet a growing number of studies (e.g., O'Neill & Biederman, 1974; Overmier & Payne, 1971; Scavio & Gormezano, 1980) suggest that prior CS association with an appetitive US enhances aversive conditioning with the same CS. The rats used in the present research had daily pairings of darkness and food prior to the start of an experiment (i.e., the rats typically did most of their feeding during the dark phase of the light/dark cycle). Although it might be predicted that this past experience with pairings of darkness and food would carry over to the experimental setting in which darkness signaled a food pellet (Group L-/D+, Experiment 3), the interaction experiments suggest that such experience may have also resulted in the enhanced performance when darkness was paired with a shock US (Group L-/D+, Experiments 1, 2, and 4).

In Experiments 1 and 4 it is possible that the rats used cues other than light and dark in acquiring the discrimination between the S+ and S- conditions. In each of these studies, the light and dark CSs were the phases of the light/dark cycle. In the freely feeding rat, deprivation state also varies as a function of the light/dark cycle, with higher levels of deprivation experienced more often during the light phase than during the dark phase (e.g., Richter, 1965). The rats used in Experiments 1 and 4 may have relied on deprivation cues rather than, or in addition to, illumination cues as predictors of shock. Davidson (1987) observed the freezing response and found that rats could use deprivation cues as discriminative signals for shock. The rats used in his studies were able to perform the discrimination when the deprivation CSs (0 and 4 h) simulated conditions that might be experienced under free-feeding conditions (Collier et al., 1972).

In addition to deprivation cues, the rats in Experiments 1 and 4 may have used any of a number of endogenous cues that are known to have circadian rhythms. So, for example, rats in Group L+/D- may have used the daily drop in body temperature (e.g., Richter, 1965) or the multitude of changes related to slowed metabolism (e.g., Philippens, Mayersbach, & Scheving, 1977) as predictors of shock. The fact that Group L+/D- failed to learn the discrimination when only illumination cues were present (Experiment 2), but was successful when endogenous cues were available as signals (Experiments 1 and 4), suggests that the rats

in Experiments 1 and 4 may have been using the endogenous aspects of phase rather than the exogenous aspects of phase as predictors of shock.

It should also be noted that the results of Experiment 1 differed from those of related studies conducted in Collier's laboratory. Jensen et al. (1983) investigated the effects of differential procurement or handling requirements (i.e., bar presses) during the light and dark phases. Their data indicated that the relation between meal frequency/meal size and procurement cost depended on the phase of the light/dark cycle. Rats decreased the frequency of meals taken during the light phase to zero when the cost of procuring a meal in that phase reached FR640. This changeover did not occur for dark phase feeding until the procurement cost was raised to FR2560. In other words, Jensen et al. found an asymmetry in the relation between light/dark feeding and procurement cost in the direction opposite to that which was found when the cost was the risk of shock. The discrepancy between the findings reported by Jensen et al. and those of Experiment 1 may be caused by the type of cost manipulated in the two studies. In the study conducted by Jensen et al., the amount of work (i.e., bar presses) required to procure a meal was manipulated in the light and dark phases. In Experiment 1, cost was varied over the two phases in terms of the time the rat spent at risk of shock while feeding.

This opposition of outcomes as a function of cost manipulation may provide insight into the functional role of nocturnal feeding in the rat. The finding that foraging behavior was most disrupted when shock was paired with the dark phase did not support the assumption that nocturnal feeding in the rat is a defensive strategy. The report by Jensen et al. that meals taken in the light were eliminated at relatively low bar-press procurement requirements indicates that the present results with shock were not the consequence of the rat's inability to forfeit its infrequent daytime meals. Furthermore, Jensen and colleagues' finding that large bar-press requirements were tolerated in the dark suggests that the availability of food resources, rather than the risk of predation, may be an important factor favoring the rat's nocturnality.

Although a number of factors including predation pressure may have contributed to the evolution of the rat as a nocturnal species, the results of the experiments reported here did not provide support for the idea that nocturnality in the rat of the present time is a defensive strategy. Fanselow et al. (1988) suggest that in order to test functional hypotheses one must make a plasticity assumption that, "if a given behavior evolved because it enhanced biological fitness in the face of a particular environmental factor, then that behavior is likely to be plastic in response to actual (or simulated) variations in that environmental factor" (p. 372). Using that assumption they provided evidence that certain aspects of meal pattern (meal size and frequency) are plastic in response to the risk of electric shock during foraging and feeding. If the rat feeds more in the dark phase than the light phase as a predator

avoidance strategy then the plasticity assumption suggests that this pattern should be readily exacerbated when a risk factor is added to the light phase component, but this was not the case. Therefore, what we can say here is that nocturnality is not a defensive reaction to the extent that it is unresponsive to proximal risk factors. This is in marked contrast to other defensive behaviors which are highly responsive to immediate environmental risk (see Fanselow & Lester, 1988 for a review). It is possible that in the ultimate sense rats, as a species, became nocturnal because of selection pressure exerted by predators and therefore are already as nocturnal as predatory pressure demands. In other words, the animal is already maximally nocturnal. If this were the case, then one would not expect increased risk to suppress daytime feeding further. However, this assumption is difficult to test and in addition is not corroborated by two findings. Daylight feeding is readily suppressed by environmental variables that are not related to risk (Jensen et al., 1983; Panksepp & Krost, 1975; Spiteri, 1982; Vilchez & Echave Llanos, 1971) and other aspects of meal patterns are readily changed by the same sort of risk that was imposed here (Fanselow et al., 1988).

The research described here also did not lend support to the related hypothesis that rats form selective associations between light and aversive events. Rats that had light paired with shock only learned the relation when endogenous cues were available as discriminative signals for shock. The present findings corroborated those of others who suggest that the rat is unable to use illumination cues as signals for the occurrence of shock (Jacobs & LoLordo, 1977, 1980) and that fear does not condition well to a light CS (Sigmundi & Bolles, 1983; Sigmundi et al., 1980).

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